



Research paper

Does precipitation affects soil respiration of tropical semiarid grasslands with different plant cover types?



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ABSTRACT

Examination of the effects of altered precipitation and atmospheric temperature patterns on ecosystem processes are an active area of research. Influences of these climate factors may change when plant cover and species composition are disturbed as a consequence of land use change altering ecosystem processes, such as soil respiration. We addressed the following question: how does experimentally manipulated reduction in the size of each precipitation event influence soil respiration fluxes (Rs) in a tropical semiarid grassland with different plant cover and species composition? Rainout shelters were installed over eight yr old planted monospecific plots (4 m²) of *Bouteloua gracilis*, the keystone species of the grassland biome, and over mixed grassland plots in sites that recovered from abandoned agricultural land, allowing full or a 50% reduction of ambient precipitation. Soil respiration rates as well soil temperature (T_{soil}) and soil water content (SWC), as controlling factors, were monitored. Overall, SWC was the most important control for Rs explaining ~70% of its variability, followed by T_{soil} which explained ~25% and plant cover type having a minor effect (3%) explaining Rs variability. Still, Rs exhibited differential responses when comparing plant cover types; SWC in the mixed grassland had up to 90% relative influence on Rs as compared to 10% by T_{soil}. In contrast, Rs rates in monospecific *B. gracilis* plots exhibited less overall variability considering SWC (55–60%) and T_{soil} (40–45%), suggesting that grasslands dominated by the keystone species are more resilient and better buffer the effects of extreme climatic drought conditions on ecosystem processes.

1. Introduction

Drylands comprise a wide diversity of ecosystems that cover ca. 40% of the terrestrial surface (Lal, 2004). Generally, precipitation (PPT) patterns in drylands are characterized by their scarcity and the high intra and inter-annual variability, in which small rainfall events in form of “pulses” account for a large proportion of annual water inputs (Sala and Lauenroth, 1982). Interannual variability in PPT across drylands spans such a large range that rainfall events are considered hot spots, as they control the variability in regional carbon fluxes (Jung et al., 2011; Blazewicz et al., 2014). Ahlström et al. (2015) have reported that it is this high variability in PPT that controls the interannual variability of the global C sink. Global circulation models forecast that the arid and semiarid regions will have a 10 and a 20% reduction of summer and winter PPT, respectively, by the end of the 21st Century (Christensen

et al., 2007) i.e., under current CO₂ emission scenarios. Scenarios also project larger PPT events with longer periodicity (occur less frequently) (Easterling et al., 2000; Houghton, 2001). These expected changes in climate change drivers (i.e. air temperature and precipitation regimes) are projected to increase soil respiration rates globally, i.e., it will increase C losses from the ecosystem (Schlesinger and Andrews, 2000).

Land use change is attributed to the 12.5% of total CO₂ emissions to the atmosphere at the global scale (Houghton et al., 2012; IPCC, 2013). While land use change is usually described as conversion or modification of land cover (Chapin et al., 2011) to increase the production of a certain commodity, with clear impacts on ecosystem structure and function, relatively little is known about land abandonment and its legacy effects on fundamental ecosystem processes (Foley et al., 2005), as those on the biogeochemical and biophysical fluxes, including, the cycling of carbon, water, energy. Previous studies have demonstrated that

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shifts in plant cover or dominant species may alter the net radiation budget and ecosystem energy balance (Chapin et al., 2008; He et al., 2015). Similarly, changes in species composition has been associated with changes in soil mineralization processes (Steltzer and Bowman, 1998), hydrological fluxes (Pérez-Suárez et al., 2014), and photosynthesis and respiration rates (Delgado-Balbuena et al., 2013).

In this context, a change in plant cover that induces variations in the energy balance, the hydrological cycle and in the amount and quality of organic matter, suggests that factors such as soil temperature and soil moisture that control soil respiration rates may also concurrently change (Raich et al., 2002; Raich and Schlesinger, 1992). Other factors that control soil respiration rates include; soil organic matter quality and quantity (Taylor et al., 1989), root and microbial biomass, root nitrogen content (Ryan et al., 1996), soil acidity, soil texture, and site productivity (Raich and Potter, 1995; Raich and Schlesinger, 1992). For interacting controlling factors, drought has been shown to decrease the degree of control by soil temperature, and re-enforcing the degree of control of soil water content (SWC) on Rs (Law et al., 1999; Reichstein et al., 2002), which depends principally on the magnitude and periodicity of individual rain events (Lee et al., 2002). Precipitation in the semiarid grassland biome of Mexico is characterized by predominantly small events, where ~60% of the annual PPT fall as events < 5 mm d⁻¹ (Delgado-Balbuena, 2016). In addition, during the rainy season there is a predominance of short inter-event dry periods (inter-event periods < 10 days), whereas long dry periods may last up to six to nine months (Easterling et al., 2000). PPT events that follow after a medium to long dry period coincide with pulsed losses of CO₂ from the ecosystem to the atmosphere, that are likely the result of SWC-induced activation of soil microorganisms i.e., Birch effect (Birch, 1958, 1964; Rey et al., 2002), and/or physical gas displacement of CO₂ by water in soil pore spaces (Huxman et al., 2004). Predicted changes in the PPT regime over the drylands of Mexico (Christensen et al., 2007) suggest marked alterations in ecosystem process rates controlling the cycling of CO₂, and the overall carbon balance in these semiarid regions (Delgado-Balbuena, 2016).

The tropical semiarid grassland biome in central Mexico is currently undergoing unprecedented directional changes in the abundance of its keystone grass species. *Bouteloua gracilis* populations have declined due to massive conversion of grasslands to agricultural land, urbanization, road infrastructure and overexploitation as a livestock production system. For instance, vast extensions of grassland that had been converted to rainfed agriculture about 50 to 80 years ago, have been abandoned due to harsh climatic conditions with decadal periods of drought (Arredondo et al., 2005). Several decades of vegetation recovery have led to the establishment of less grazing-palatable subordinate C₄ grass species and several C₃ annual herbs (e.g. *Muhlenbergia rigida*, *Aristida divaricata*, *B. hirsuta*, *B. scorpioides*; Arredondo et al., 2005; Medina-Roldan et al., 2007). Previous comparative studies with these transformed secondary grasslands have shown that these modified plant communities alter the fraction of total intercepted net radiation by the canopy, air temperature, and SWC (Delgado-Balbuena et al., 2013; Medina-Roldan et al., 2007). These altered grassland communities also differ in their inherent traits (Eviner and Chapin, 2003) such as specific leaf area (Delgado-Balbuena et al., 2013) and shoot and root biomass (Medina-Roldan et al., 2007), which in turn, feed back on ecosystem functions. Keystone species functional traits of *B. gracilis* reduce the incidence of solar radiation reaching the soil surface, lower near-soil air temperatures (Delgado-Balbuena et al., 2013), enhance infiltration rates of PPT, soil water retention, the efficiency in extracting soil water (Medina-Roldan et al., 2007) and exhibit higher water use efficiency (Arredondo et al., 2016) than those of altered mixed-species grasslands establishing after land abandonment.

We addressed the question on how does experimental manipulation of PPT (i.e. 50% reduction of each event) influence soil respiration rates (Rs) in mixed species grasslands on former agricultural land compared to 10 year old *Bouteloua gracilis* plots. We expected reduced PPT would

mimic natural drought and thus result in a decline in soil CO₂ emissions to the atmosphere compared to natural PPT (H1). Further, we expected reduced PPT would reduce Rs to a greater extent in altered, mixed grasslands compared to monospecific *B. gracilis* grasslands, due to warmer and drier micrometeorological conditions in the former setting (H2). Lastly, we expected experimentally reduced PPT would lessen the degree of control of soil temperature on Rs, and this effect would be greater in mixed grassland conditions with potentially higher evaporation rates compared to the *B. gracilis* grasslands (H3).

2. Materials and methods

The study was carried out at the *Vaqueries* grassland research station of the National Institute for Agriculture, Animal Production and Forestry Research (INIFAP) located in the geographic subprovince Llanos de Ojuelos, Jalisco, México (21°46'52.25"N, 101°36'29.56"W, 2240 m.a.s.l.). The study area is situated in the southernmost extension of the shortgrass steppe biome in North America (Aguado-Santacruz and García-Moya, 1998), with a topography characterized by plain terrains with gentle rolling hills (COTECOCA, 1979). Soils are Xerosols with pH values ranging between 5.5 and 6.5, and with a low content of organic matter and cation exchange capacity (Aguado-Santacruz and García-Moya, 1998). The climate is semiarid with an average of 424 mm annual rainfall over the last 30-y, with most of the PPT occurring in the summer months (July–September) and with an average annual temperature of 18 °C (COTECOCA, 1979).

2.1. Rainout shelters and plot structure

In 2011, we installed a rain manipulation experiment with rainout shelters to reduce the amount of natural annual PPT (Yahdjian and Sala, 2002) on plots (2.0 × 2.0 m) with two plant cover types: 1) 10-y old transplants of adult *B. gracilis* tussocks and 2) 70-y old mixed grassland recovered from abandoned agriculture. For each plot, V-shaped acrylic strips (0.11 × 2.2 m) without UV-filters (ACRYLITE® GP-OP4, Evonik Cyro LLC, Parsippany, NJ) were installed atop of two parallel pairs of metallic supports (2.00 m apart) at different heights (1.10 m in the back and 0.90 m in the front of plots) to obtain a slope to drain the rain (Fig. 1a). We installed nine acrylic strips per plot (1.98 m² plot cover = 49.5%) attempting to remove ~50% of each PPT event. Around each plot, a 25 cm wide aluminum sheet was inserted 15 cm into the ground to protect plots from both surface runoff and horizontal subsurface water flows from neighboring areas, i.e., other water inputs. The inclined V shaped strips drained the intercepted rain into a covered aluminum gutter that was connected by a hose to a 40 l container (Fig. 1a). The actual PPT removed on each plot was estimated as the difference between the total PPT recorded at each event with two rain gauges (mm) (All-weather rain gauge, Forestry Suppliers Inc., Jackson, MS) installed at the opposite ends of the research area, and the volume of water collected in the containers. This allowed us to account for the effects of occasional lateral storms and unintended breakage of acrylic strips.

The monospecific grassland plots included only the dominant species *B. gracilis*, whereas the mixed grassland consisted of a community of the most common species: *B. gracilis*, *B. hirsuta*, *B. scorpioides*, *Microchloa kunthii*, *Muhlenbergia rigida*, *Paspalum* sp., *Panicum obtusum*, several annual herbs and the subshrub *Isocoma veneta* (Aguado-Santacruz et al., 2002). Seven replicates were installed for each treatment combination. To account for potential artifact effects of rainout structures on local radiation and wind conditions, rainout shelters were installed on both control and treatment plots. However, in case of the control plots, the collected PPT was homogeneously applied on the control plots with a watering can the day after the PPT event.

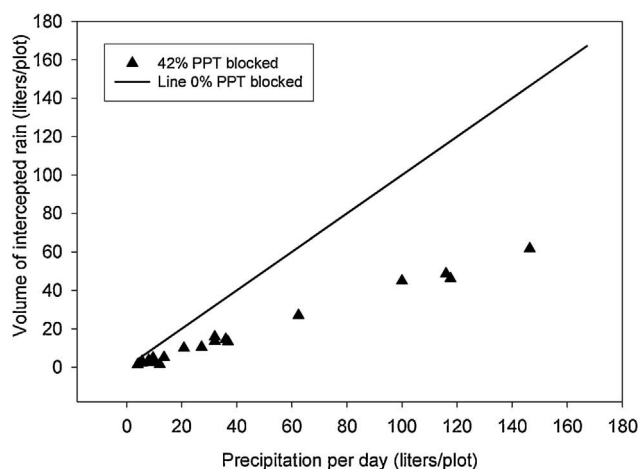


Fig. 1. An image showing a view of the rainout shelters in the mixed grassland type (a). Ambient (100%) precipitation and reduced (42%) by the acrylic structure of the rainout shelter reaching grassland plots (b).

2.2. Micrometeorology and biomass

Soil water content (SWC%) (CS-616, Campbell Scientific Inc., Logan UT) was monitored in four plots of each treatment combination and automatically recorded at 30-min intervals with a datalogger (CR23X, Campbell Scientific Inc.). On each plot, soil temperature probes (TMC50-HD, Onset, Bourne MA) were inserted at 3 cm depth and recorded at a 30-min frequency (HOBO U12 temperature datalogger, Onset). Soil respiration (R_s) was measured once a month, using a gas exchange system (LI6400 XT, Li-Cor Inc., Lincoln, NE) that was connected to a soil CO_2 flux chamber (LI6400-09, Li-Cor Inc.). On each plot, a week before the start of R_s measurements, a PVC ring 12 cm diameter and 3 cm tall was inserted 1 cm into the soil. Around the top ring rim a rubber strip was attached to help seal the LI6400-09 chamber to the PVC ring. For R_s measurements, the chamber was set on top of the ring to then record changes in CO_2 concentration inside. For this, we first we lowered the CO_2 concentration inside the chamber to a user-defined concentration (5–10 $\mu\text{mol CO}_2$ below ambient $[\text{CO}_2]$), and then started measuring CO_2 increase within the chamber due to R_s . The slope of the change in CO_2 concentration versus time was considered the R_s rate. Each monitoring period lasted for around 5 min and automatically ended when R_s parameters got stable. This procedure was carried out three times during the day for each plot at each monitoring date for a whole year.

2.3. Data analysis

For this study, we examined the effect of grassland type (natural *B. gracilis* cover, mixed grassland) and precipitation amount (control = ambient, 50% experimental reduction) on R_s and its principal abiotic controlling factors T_{soil} and SWC. Two-factor analysis of variance (grassland by precipitation treatment combinations) was used to examine the effects on soil temperature (T_{soil}) and SWC and CO_2 fluxes; we applied MIXED models with repeated measures arrangement. However, due to the arrangement of grassland type sites, we had limitations for randomization to implement for instance a blocking or split plot design. We are confident we did not face pseudo-replication problems; previous studies examining autocorrelation patterns in semiarid ecosystems with geostatistical tools reported that biogeochemical processes in similar ecosystems differ within spatial distances less than a meter (Loescher et al., 2014; Jackson and Caldwell 1993). In this way, we also maintained consistency across all plots of other environmental conditions, such as soil texture, soil depth, landscape position, genetic pool of grasses, to reduce additional confounding factors. This limitation for randomization has been faced in similar studies and solved similarly (Chen et al., 2008; Talmon et al., 2011).

The Shapiro-Wilks test was used to examine normal distribution in log-transformed values of soil respiration, soil temperature and soil water content. Post hoc comparisons of treatment means were carried out using least square means comparison test. Linear relationships among R_s fluxes and the environmental controls, SWC and T_{soil} were examined with a type I regression analysis. To compare slopes of the regression analysis for R_s on a basis of sampling time as a function of environmental factors a test of slope homogeneity was used. This test permitted to compare R_s for each of the different treatment combinations. All statistics were carried out using the SAS statistical software (University edition, SAS Inc. Cary NC.).

To fit R_s to T_{soil} Van't Hoff's exponential model was used (Hoff and van't, 1898),

$$R_s = R_b \exp(k \cdot T_{\text{soil}}) \quad (1)$$

where, R_s is the soil respiration rate, ($\mu\text{mol m}^{-2} \text{s}^{-1}$) that depends on T_{soil} , and R_b refers to basal respiration rates, and k is a rate constant. The R_s exponential model was linearized such that,

$$\ln(R_s) = \ln(R_b) + k \cdot T_{\text{soil}} \quad (2)$$

where $\ln(R_s)$ and $\ln(R_b)$ is the natural logarithm of R_s and basal respiration (R_b), respectively.

Then, the sensitivity of R_s to the T_{soil} increase (Q_{10}) was calculated as,

$$Q_{10} = \exp(10 \cdot k) \quad (3)$$

Whereas, a linear regression was used to estimate the relationship between R_s and SWC,

$$R_s = y_0 + b \cdot \text{SWC} \quad (4)$$

where y_0 and b are estimated parameters.

To test the relative contribution and interactions of T_{soil} and SWC on R_s , a boosted regression tree (BRT) analysis was performed. A full model that included all treatments/variables/time was used for detecting main variables (SWC, T_{soil}) – factors (PPT treatment, plant cover) controlling R_s . To test the changes in the contribution from each of the environmental controls on R_s by treatment, individual BRTs were carried out for each PPT x grassland type treatment combination. A slow learning rate ($lr = 0.005$), tree complexity = 5 and a bag fraction = 0.75 were the parameters used in the full model. For individual treatment combination BRTs, the tree complexity was reduced to 3 and a bag fraction was 1, because of sample size reduction resulting from treatment splitting. The “gbm” package for R statistics software (R Core Team, 2014; Ridgeway, 2015) was used for these analyses.

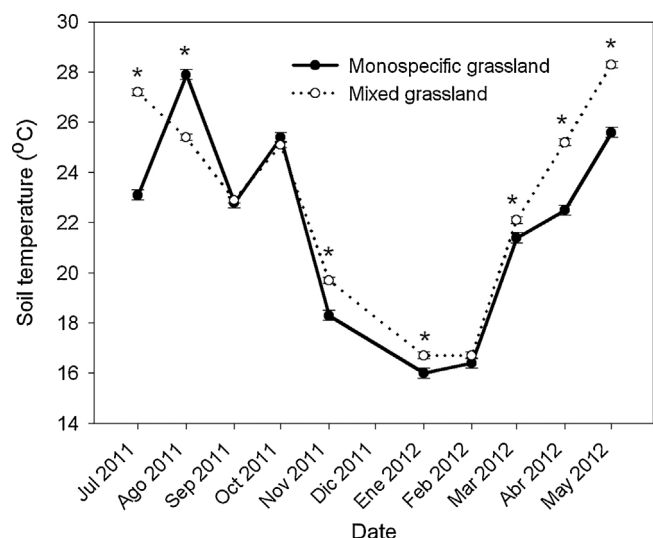


Fig. 2. Annual time series of soil temperature (T_{soil}) recorded in plots of either monospecific *B. gracilis* or mixed species grassland type (GT x Time). Points represent the average of seven replicates and bars indicate ± 1 S.E.

3. Results

3.1. Effect of PPT and grassland type on soil abiotic variables

Annual total precipitation for 2011 was 282 mm, the lowest on record for the past 70 y. Due to acrylic leakage and wind effects, the actual intercepted PPT by the rainout shelter was reduced by 42% instead of the designed target of 50% (Fig. 1b). Thus, in the reduced PPT treatment total annual cumulative PPT was 164 mm y^{-1} . Approximately 60% of the total annual PPT fell in events $< 5 \text{ mm}$, the remaining 40% in events $> 15 \text{ mm}$; 70% of the inter-rainfall periods lasted < 5 days (Delgado-Balbuena, 2016).

We observed monthly differences in average T_{soil} between the two grassland types (GT x time $P < 0.0001$, Fig. 2), with higher T_{soil} in the mixed grassland treatment during the dry months, but similar T_{soil} under wet soil conditions. Soil temperature (T_{soil}) differed significantly between PPT treatments ($P < 0.0001$, Table S1), with the reduced PPT presenting higher T_{soil} (22.7°C vs 22.1°C for 42% reduced and control, respectively). We also observed differences in SWC in the trajectory of the year when comparing grassland type (GT x time $P < 0.0002$, Fig. 3); the mixed grassland treatment had 1–2% lower SWC than *B. gracilis* monospecific plots, during the dry months. No differences occurred in response to PPT treatments or any other interactions (Table S2).

3.2. Response of soil respiration to environmental factors

Soil respiration differed in the two grassland types at different dates of the year (GT x time, $P < 0.0001$, Fig. 4) with the mixed grassland treatment exhibiting higher Rs rates than the monospecific *B. gracilis* grassland during the dry months (November to April). Using the linearized expression of the exponential model (Eq. (2)), Rs responded to changes in T_{soil} in both grassland types, but the degree of this response varied seasonally ($R^2 < 0.35$) with steadily declines after rain events. According to the slope homogeneity test, Rs was highly responsive to SWC, however this depended on grassland type and PPT treatment ($P < 0.05$, Table S4, Fig. 5). Slope differences (i.e., Rs rates) differed between grassland types on the first and sixth sampling dates ($P < 0.05$), when *B. gracilis* grassland exhibited its highest and lowest Q_{10} values, respectively (2.7 and 0.97 compared to 1.4 and 0.83 for mixed grassland type). Seasonal variation in Q_{10} was positively related with SWC in the mixed grassland ($P < 0.05$), while no such

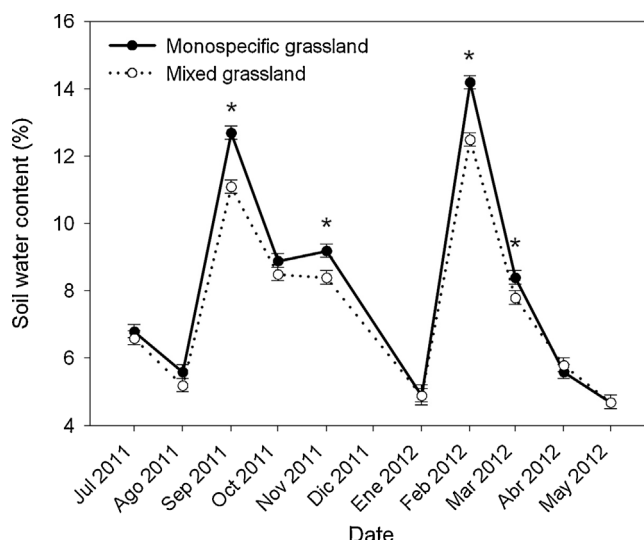


Fig. 3. Annual time series of soil water content (SWC) recorded in plots of either monospecific *B. gracilis* or mixed species grassland type (GT x Time). Points represent the average of seven replicates and bars indicate ± 1 S.E.

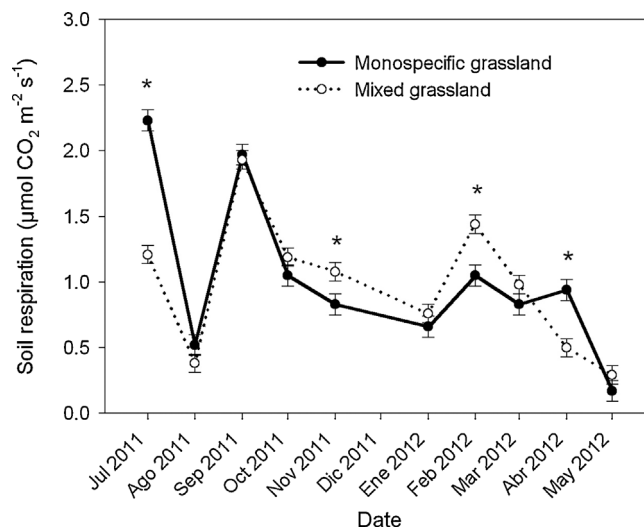


Fig. 4. Annual time series of soil respiration (R_s ; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) rate recorded in plots of either monospecific *B. gracilis* or mixed species grassland type (GT x Time). Points represent the average of seven replicates and bars indicate ± 1 S.E.

relationship was apparent in the *B. gracilis* treatment (Fig. S1). Instead, only in *B. gracilis* grassland types, basal respiration (R_b) rates and SWC were positively related (Fig. S2).

The linear regression analysis relating R_s with SWC, revealed a significant interaction considering grassland type ($P < 0.004$); while the PPT treatment remained without effect ($P > 0.05$) (Fig. 5). In particular, the test of slope homogenization showed that the R_s rate increased significantly more with increasing SWC in mixed compared to monospecific grassland plots ($b = 9.57 \pm 1.74$, $R^2 = 0.23$, $P < 0.0001$; and $b = 14.74 \pm 1.27$, $R^2 = 0.53$, $P < 0.0001$, for monospecific (*B. gracilis*) and mixed grassland types, respectively).

Boosted regression trees (BRT) showed a cross validation correlation $> 77\%$. Partial dependence plots demonstrated an increases in R_s rate with a rise in SWC at a range of 4%–12%, where the asymptote is reached (Fig. 6a). In case of T_{soil} , R_s rates increased at a maximum rate at 31°C followed by a reduction in R_s at higher T_{soil} (Fig. 6b). The full BRT model revealed that SWC was the most important variable controlling R_s rates accounting for 70% of its variability. T_{soil} was the second most important variable explaining 25% of the observed

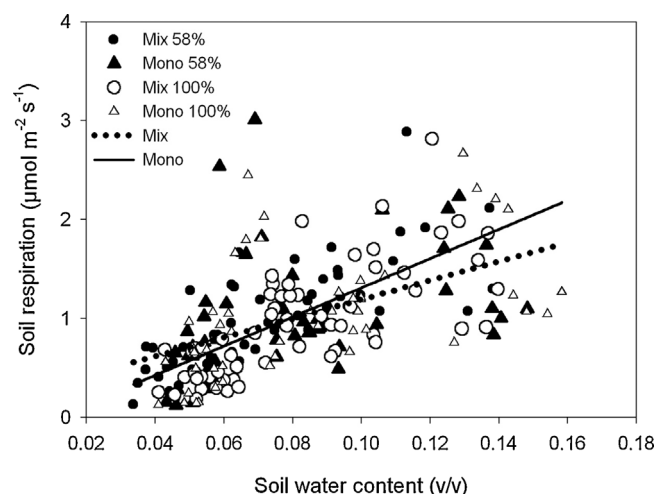


Fig. 5. Comparison of slopes for the linear relationships between soil respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and soil water content (%), as a function of grassland cover type (monospecific and mixed) and incoming precipitation (100 and 58%). Points represent individual records of soil respiration. Slopes between precipitation treatments were not different ($P > 0.05$). Solid and dotted lines correspond to regression lines for mixed and monospecific grassland types, respectively.

variability in Rs. Grassland type and PPT contributed with only 3.2% and 0.9%, respectively, to explained variance of Rs (Fig. 6c). Still, a slight increase in Rs was observed under the mixed grassland (Fig. 6d) and the 42% decreased PPT (Fig. 6e). This model also showed a significant interaction only between SWC and T_{soil} (33.4%) but not with other variables ($< 2\%$, Fig. 6f).

Boosted regression trees that tested PPT x plant cover types showed changes in the relative contribution of SWC and T_{soil} on Rs. Soil respiration in the mixed grassland was more responsive to SWC than to

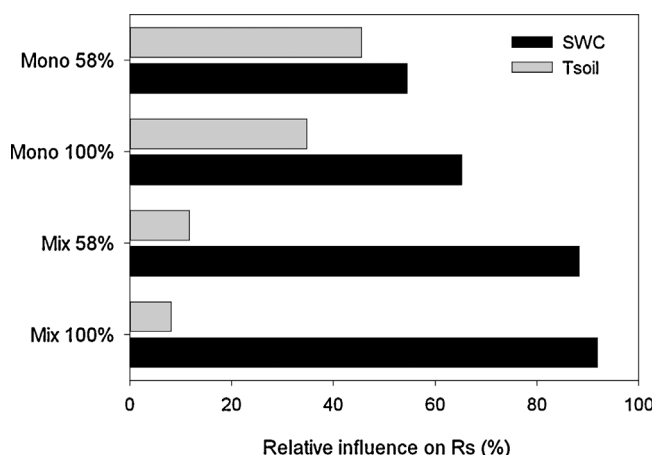


Fig. 7. Relative influence of soil water content (SWC) and soil temperature (T_{soil}) on soil respiration corresponding to grassland types (Mix = mixed, and Mono = monospecific grassland stands) and precipitation treatment (100% and 58% of current PPT).

T_{soil} changes (88% and 12% for SWC and T_{soil} , respectively), whereas the degree of control by SWC and T_{soil} on Rs in the *B. gracilis* treatment was almost equal (54.5% and 45.5% for SWC and T_{soil} , respectively, Fig. 7). In general, the PPT treatment exerted slightly more control on Rs compared to T_{soil} , independent of plant cover type (3 and 10% of increase for mixed and *B. gracilis* treatments, respectively).

4. Discussion

4.1. Influence of precipitation reduction on Rs

The study year coincided with the most extreme drought recorded for the last 70 y. Interestingly, even a reduction of natural PPT by 42%,

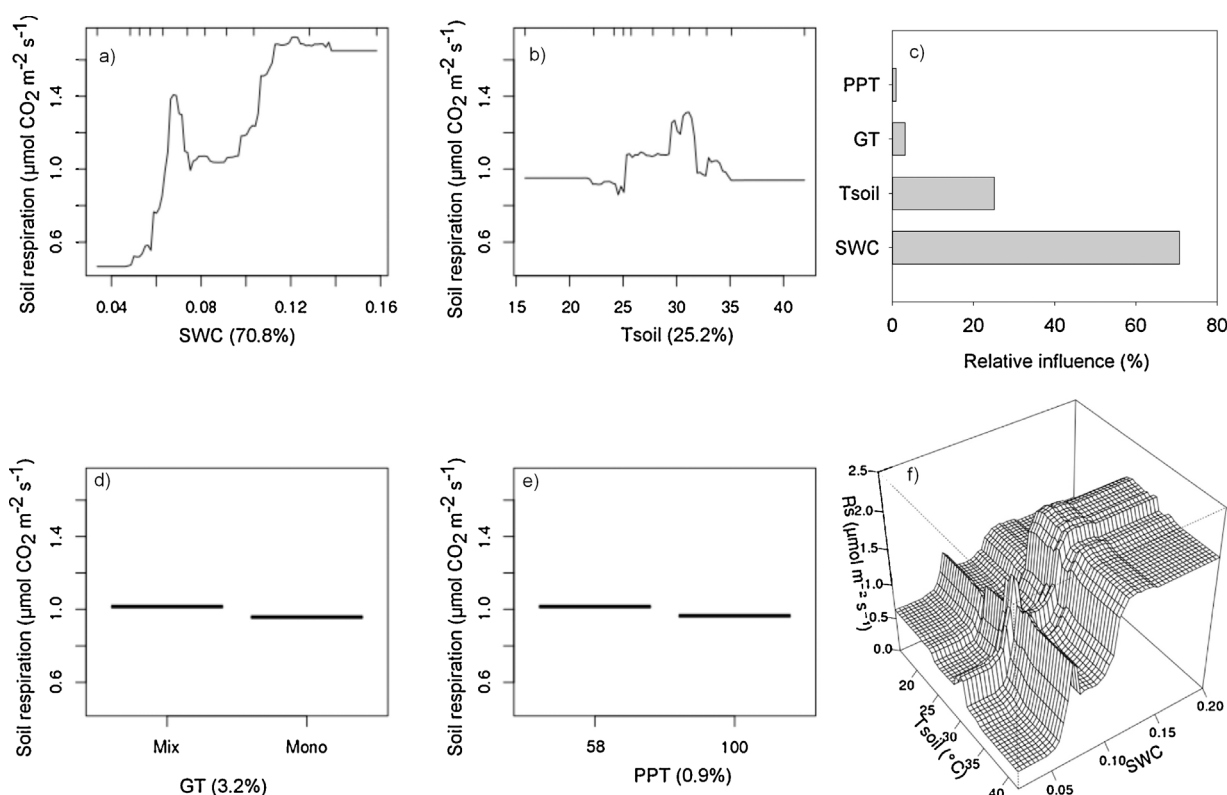


Fig. 6. Partial dependence plots for soil respiration (R_s , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) as a function of soil water content (a), soil temperature (b), grassland type (d), and precipitation treatments (e), averaging the effects of all other variables. The relative contribution (%) of predictor variables to Rs is shown in (c), and R_s variability as a result of the different combinations of SWC and T_{soil} (f).

did not seem to translate into a significant drop in SWC at 15 cm soil depth compared to ambient PPT (Table S2). We attributed this response to, i) a high water holding capacity of the upper soil layer, in particular when SWC drops below 12%. Beyond this threshold, for every 1% decline in SWC there is a corresponding drop in ~ 4 bar in soil water potential (Fig. S3), meaning that it becomes harder and harder to lose water, ii) the likely role of the caliche layer as a potential source of water may become more apparent as a buffer under extremely dry conditions (Duniway et al., 2010), iii) the PPT pattern events during the study that were apparently large enough to recharge the subsoil even at the reduced PPT treatment, and iv) linked to the previous mechanism, the observed PPT pattern during the experiment consisted of short inter-PTT periods (Fig. S4). All these previous factors suggest that several large and consecutive PPT events like the ones observed in 2011 and at the beginning of 2012 might be more important explaining xeric ecosystem hydrology and function as previously thought, as they seem more effective recharging the subsoil and thereby maintain the SWC above a water stress threshold (the “soil water bucket” model, (Gordon and Famiglietti, 2004; Knapp et al., 2008)). During the study, four large consecutive PPT events accumulated 95 mm within four days (Fig. S4), suggesting that drought tolerance of this biome might be directly coupled to extreme meteorological conditions that contribute to both deep infiltration possibly reaching the caliche layer (at maximum 50 cm depth) and a relatively high water retention potential of the soil and an impermeable underlying rock-like substrate that functions as a crucial temporary water reservoir (Duniway et al., 2010). Our results support the urging call for more realistic climate change simulations including the manipulation of precipitation frequency, intensity and seasonality, since PPT patterns are also expected to shift towards fewer and more extreme events (Knapp et al., 2015; Liu et al., 2016).

The lack of effect of the PPT reduction treatment on Rs rates lead us to reject H1. Nevertheless, SWC a variable ultimately depending on PPT was the most important control of Rs. In these grassland types, a comparatively low minimum soil humidity level seems to stimulate soil activity suggesting soil microbial communities are highly responsive to extremely low SWC threshold levels as Rs was activated at only 4% (Fig. 6a). Equally unusual was the high responsive capacity of soil organisms and root activity as Rs rates increased rapidly with increases in SWC. The upper threshold of Rs was reached at about 12% SWC, beyond that Rs rate remained constant. Causes for reaching this threshold could be associated with potential anaerobic conditions, or low biomass accumulation of microorganisms and roots. This kind of threshold has been observed also at the ecosystem respiration (ER) level, in the same grassland using the eddy covariance technique (Delgado-Balbuena, 2016).

4.2. The role of grassland type on Rs

Grassland cover type greatly influences grassland soil hydrology (Medina-Roldan et al., 2007) by regulating runoff, infiltration rate, and percolation of rain water. In this study, *B. gracilis* grassland cover maintained overall higher SWC and lower T_{soil} (Figs. 2 and 3) than the mixed grassland cover throughout the experiment, favoring in the mixed grassland comparatively higher Rs rates compared to the *B. gracilis* grassland (supporting H2). These microclimatic conditions in the mixed grassland plots (Figs. 2 and 3), may have resulted from a combination of larger soil interspace area, lower stature, and lower soil organic matter content of the mixed grassland, which in turn resulted in larger evaporative losses. Medina-Roldan et al. (2007) showed that along a livestock grazing intensity gradient with a monodominant *B. gracilis* cover at the moderate end and a mixed species cover at the high-intensity side, had less soil organic matter, lower plant cover, and less belowground biomass when grasslands were disturbed. Similarly, Delgado-Balbuena et al. (2013) comparing monodominant *B. gracilis* to mixed disturbed grassland showed that there was an increase in the amount of radiation reaching the soil surface and a decrease in SWC.

These previous observations from established grassland ecosystems support our observations. Still, the relative contribution of grassland type to explain variability in Rs rates was relatively low (i.e., 3.2% of the total, Fig. 6c and d). In this study, Rs in mixed grassland types showed greater variability when exposed to high fluctuations of the controlling factors (i.e., it was more sensitive to changes in T_{soil} and SWC) than in monospecific stands (Fig. 7). This greater sensitivity might be related to comparatively greater extensions of plant interspaces in the mixed grassland, which then translates into greater exposure to radiation, and accelerated cycles of desiccation, increase in T_{soil} , sensible heat flux and re-wetting.

4.3. Soil respiration and environmental drivers

Many studies have shown that T_{soil} and SWC are the two main controls of Rs in dryland soils, with T_{soil} being a continuous variable, and PPT being a stochastic variable inducing the recharge of soil water. Respiration from plant roots and soil organisms requires an optimal SWC to be sustained, however in drylands SWC may drop below this optimal value, though we did not detect it in our study. In more hydric ecosystems however, high SWC may fill up all pore space and switch soil organisms with an aerobic to those with an anaerobic metabolism (Horz et al., 2004). Under drought conditions however, the effects of low SWC on Rs can covary with T_{soil} , reducing the degree of variability in Rs explained by T_{soil} Eq. (1), resulting in SWC having more control on Rs (Law et al., 1999; Loescher et al., 2006; Reichstein et al., 2002). In this study, the relative influence on Rs was higher by SWC than by T_{soil} (Fig. 6c). Thus the BRT analysis showed the SWC was the main control for Rs variability, but with its importance decreasing in the *B. gracilis* treatment and under reduced PPT, thus coinciding with H3.

The larger dependence of Rs on SWC in the mixed grassland condition may follow structural and physiological plant-microbial characteristics and lower root biomass (Medina-Roldan et al., 2007), making the resultant vegetation more sensitive to drought and requiring a higher SWC threshold for activating Rs. The sensitivity of Rs to T_{soil} (Q_{10}) was positively related with SWC in mixed grasslands, and increased Rs from these communities under moist soil conditions. In contrast, in *B. gracilis* stands basal respiration (R_b) was related to SWC but not to Q_{10} , i.e., Rs in *B. gracilis* plots was less sensitive to SWC changes. Thus, whereas basal respiration is a multiplicative term, its temperature sensitivity is exponential. Apparently, more seasonally variable ecosystems (e.g., deciduous forests) and those with larger carbon pools have larger variance in carbon cycling rates that are expressed in the change in basal respiration rates rather than Q_{10} response (Curiel-Yuste et al., 2004).

Decades of increased social and economic pressure on these arid and semi-arid ecosystems have resulted in changes in plant communities and losses of soil carbon (Medina-Roldan et al., 2007; Medina-Roldan et al., 2008). More specifically, the semiarid grassland from Mexico decreased spatially from 11% in 1978 (Rzedowski, 1978) to a 6% in 2002 (Velázquez et al., 2002) mostly as a consequence of land conversion to agricultural use, mostly rainfed agriculture. While not all converted land has yet been accounted for in explaining declines in grassland C stocks, yet an even larger gap of information in the C cycle is related to the fraction of C losses related to formerly converted grassland and recently abandoned agricultural land, as these mixed grasslands experience a significant reduction in abundance of the native ‘keystone’ species, *B. gracilis*. *Bouteloua gracilis* as keystone species exhibits both a set of functional effects and responses patterns reflecting a highly adaptive ecosystem response portfolio to long evolutionary past characterized by highly variable and extreme climatic conditions. From the individual, population, community and ecosystem level, the above and belowground structure of *Bouteloua gracilis* greatly enhances the ecohydrological process of water infiltration, soil water retention, and plant water uptake, thereby buffering potentially growth-limiting extreme unfavorable microclimatic conditions. This species

ecohydrological effect permits *B. gracilis* on the one hand to maintain rather constant low rates of Rs coupled to relatively high rates of aboveground productivity, resulting in a net C gain (Delgado-Balbuena et al., 2013) and on the other hand, under extremely dry conditions – as in the experimental year – maintain soil activity. In this latter case, the contribution of this response pattern at the extreme ends of SWC to net ecosystem productivity still needs to be tested. A change in grassland plant species composition and structure at expenses of the key species appears to trigger higher fluctuations in Rs rates during the dry and wet seasons. Decline or loss of *B. gracilis* in the grassland biome will translate into a loss of native ecosystem function (Medina-Roldan et al., 2007) and likely its ability to recover after human-induced disturbance, i.e. resilience. This is profound given that land use and other changes in the environment (nitrogen deposition, climate change, etc.) are now chronic disturbances, rather than discrete disturbance events or inherent natural disturbance regimes under which these ecosystems evolved (Smith et al., 2009). The intricate balance in ecosystem processes that these dryland ecosystems exhibited for eons might have been substantially altered and we are witnessing future changes that we are still not able to anticipate.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.agee.2017.09.034>.

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